Birds of Lake Naivasha 2. Foraging niches and relationships between migrant and resident warblers in papyrus swamp

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Much discussion has centred on the relationships between Palaearctic migrants and African resident species during the northern winter months. The relative abundance of migrants to residents and the preferred habitats of migrants have been particularly emphasized (e.g. Morel 1968, Moreau 1972, Pearson 1972, Britton 1974).

The coexistence of migrants and residents during the winter provides much potential for competition or segregation, although unfortunately rather few data are available on this subject. Sometimes a super-abundance of food may permit coexistence of closely related migrant and resident species; this was suggested as a possible reason for two species of wagtail—the resident Mountain Wagtail *Motacilla clara* and the Palaearctic Grey Wagtail *M. cinerea*—feeding together on the same highland streams with no obvious signs of aggression or differences in foraging behaviour (Tyler & Ormerod 1986,1987). As an alternative, segregation could result. The partitioning of resources, by using different foods or habitats or by using a habitat in different ways, has been described during the breeding season (Lack 1970); between migrants in their winter quarters and morphologically similar resident species (Moreau 1972); and in some species during autumn migration (Bibby & Green 1981, Bairlein 1981, 1983, Ormerod 1990).

Acrocephalus warblers have, in particular, received attention during the breeding season and in the autumn in Europe. Here, most *Acrocephalus* spp. favour wetland habitats, notably reed-swamp dominated by *Phragmites australis*, marshes and fens. In the winter in Africa some species of *Acrocephalus* may, however, occur well away from water although others occur in abundance in lakeside vegetation (Britton 1974, 1978, Pearson 1972). In papyrus *Cyperus papyrus* swamp at Lake Naivasha in the Kenyan Rift valley up to six *Acrocephalus* warblers and three other closely related species overlap between January and March (Tyler *et al.* 1991). Papyrus swamp is consequently an interesting area for a study of resource partitioning.

In this paper data are provided on the segregation of warblers within papyrus swamp at Lake Naivasha. Particular attention is given to differences in size, in foraging behaviour and in niches favoured by each species.

Methods and study area

The study area at Lake Naivasha and methods used to catch warblers in and at the edge of the papyrus swamp have been described by Tyler *et al.* (1991). From January to early March 1990 mist-netting was carried out over a two to three day period at two weekly intervals. In late February and early March, the location of each bird caught in the nets (numbered from lake to swamp edge) and its position in the nets (bottom to top shelf) were also recorded. A note was made of all retraps of ringed birds. Casual observations were made of feeding behaviour of the swamp birds.

Results

Warbler community

During the study period a total of 234 Lesser Swamp Warblers *A. gracilirostris* was caught with 74 Sedge Warblers *A. schoenobaenus*, 20 Great Reed Warblers *A. arundinaceus*, 30

Table 1. *Body-mass, wing- and bill-lengths of eight species of warbler using papyrus swamp and swamp-edge at Lake Naivasha, January–March 1990*

Species	body-mass (g)				wing-length (mm)				bill-length (mm)		
	n	range	mean	S.D.	*n*	range	mean	S.D.	*n*	range	mean
Agra	221	11.9–21.2	16.49	1.52	223	63–79	71.74	2.75	157	12.5–18.0	15.0
Asch	68	9.2–13.5	11.41	0.95	70	63–71	67.36	1.79	23	10.5–12.5	11.4
Asci	3	10.7–11.2	11.00	0.26	4	67–71	69.5	1.73	1	13	–
Aaru	17	28.5–34.3	31.10	1.85	18	86–99	95.39	3.09	3	18	18
Abae	8	7.4–8.6	8.10	0.44	8	52–57	54.38	1.77	–	–	–
Bbab	19	10.4–13.5	11.85	0.75	19	54–67	56.74	2.84	5	12	12
Cgal	28	9.8–16.3	12.25	1.93	28	52–67	57.25	4.16	5	11–13	12
Chun	2	14.9	14.9	–	2	59–65	62.00	4.24	–	–	–

Key: *Agra* = *Acrocephalus gracilirostris*, *Asch* = *A. schoenobaenus*, *Asci* = *A. scirpaceus*, *Aaru* = *A. arundinaceus*, *Abae* = *A. baeticatus*, *Bbab* = *Bradypterus baboecala*, *Cgal* = *Cisticola galactotes*, *Chun* = *C. hunteri*

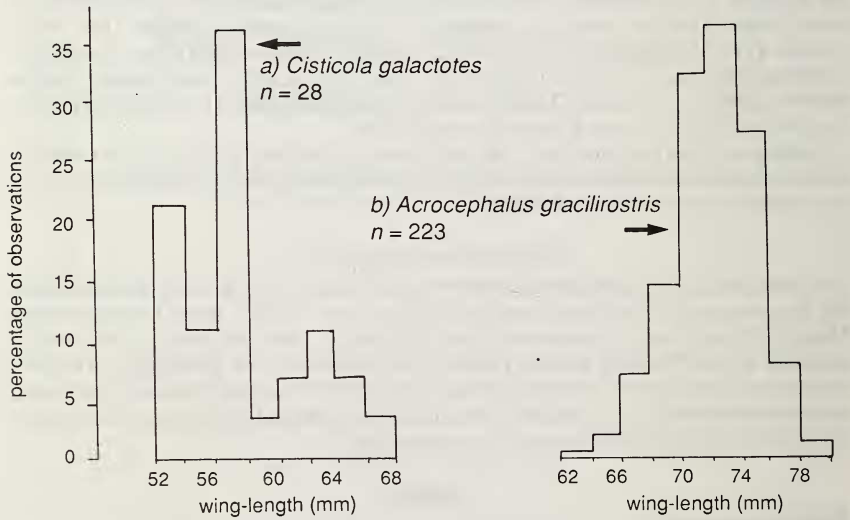

Figure 1. *Range in wing-length (mm) of a) Winding Cisticola* (n = *28) and b) Lesser Swamp Warbler* (n = *223) caught at Lake Naivasha in February and March 1990*

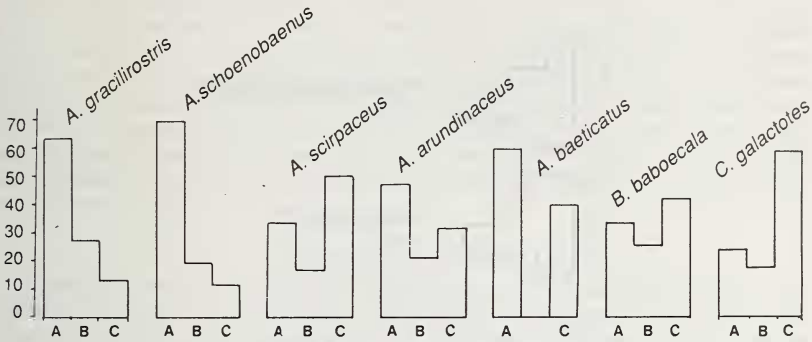

Figure 2. *Horizontal distribution of seven species of warbler caught in lakeside swamp at Naivasha. The proportion of birds caught for each species is given for three* c. *30-m lengths of nets: a) closest to the lake, b) within the swamp vegetation, and c) on the landward edge into flooded grassland*

Winding Cisticolas *C. galactotes*, 18 Little Rush Warblers *B. baboecala* and fewer than ten each of the remaining species of warbler (African Reed Warbler *A. baeticatus*, Reed Warbler *A. scirpaceus*, Basra Reed Warbler *A. griseldis* and Hunter's Cisticola *C. hunteri*— see Table 1 of Tyler *et al.* 1991).

Body-mass and wing- and bill-lengths

There were marked differences in mass and wing- and bill-length between the resident warblers with Lesser Swamp Warblers being on average heavier and having longer wings and bills than any other species (Table 1). The Palaearctic Great Reed Warbler was clearly heavier than any of the resident or other migrant species. Some Sedge Warblers overlapped in size with the smaller individuals of Lesser Swamp Warblers.

The great range in wing-lengths in both *A. gracilirostris* and *C. galactotes* was probably due to males being larger and heavier than females, although there was considerable overlap between the sexes (Fig. 1). Individuals of *A. gracilirostris* and of *B. baboecala* at Lake Naivasha had longer wings than birds in western Kenya (see Britton 1978) although *B. baboecala* at Naivasha were lighter than those weighed by Britton.

Location and height of species within the nets

About 65 per cent of Lesser Swamp Warblers were caught in the outermost two nets i. e. close to the lake and within the true swamp (Fig. 2). This species occurred in the lakeside nets more often than Great Reed Warblers (= 10.39, $P < 0.005$) or Little Rush Warblers (= 166.39, $P < 0.001$). Sedge Warblers also occurred more commonly nearer the lake than Little Rush Warblers (= 7.32, $P < 0.005$). The sample size was rather small for African Reed, Little Rush Warblers and Great Reed Warblers but these appeared to be more dispersed, occurring both within the swamp and towards the landward edge. Winding Cisticolas occurred significantly more often on the landward edge than Lesser Swamp Warblers (= 25.07, $P < 0.001$) or Sedge Warblers (= 25.07, $P < 0.001$).

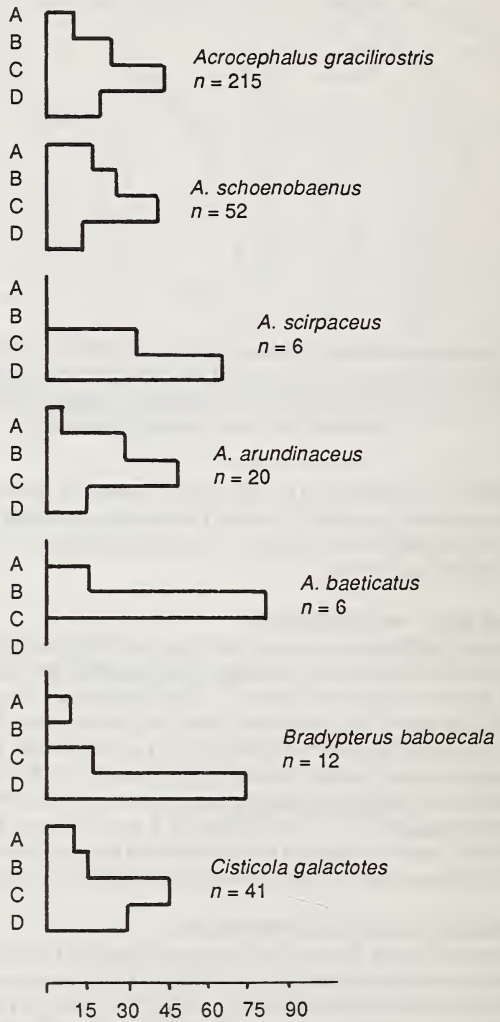

Figure 3. *Vertical distribution of seven species of warbler caught in lakeside swamp at Naivasha. The proportions of birds caught for each species are given for different net heights, described from A (top shelf) to D (bottom shelf)*

Most Lesser Swamp, Great Reed and Sedge Warblers and Winding Cisticolas were caught in the second shelf up. generally at less than 0.5 m above the ground, but occurred in all shelves (Fig. 3). Little Rush Warblers were mostly caught in the bottom shelf; on a pairwise basis, Little Rush Warblers were caught significantly more often in the lower half of the net than Sedge Warblers (= 5.35, P <0.01) and more often than Lesser Swamp Warblers at a probability of P = 0.06 (= 3.49). Winding Cisticolas also occurred more often than Sedge Warblers in the lower half of the net (= 3.94, P <0.05). In general, Little Rush Warblers occurred at lower heights than all other species but small samples limited statistical testing (Fig. 3).

Foraging behaviour

No quantitative data were obtained but opportunistic observations were made of the behaviour of any warbler seen foraging. Observations clearly were biassed towards birds feeding in the open or up in trees or the tops of the papyrus. Foraging Lesser Swamp Warblers within the papyrus stands were rarely visible but observations where the swamp met the drainage channel showed that these warblers often fed low down in the papyrus, picking insects off the water. Occasionally though they were observed feeding in the papyrus heads, where Williams (1963) also noted them foraging for flies and other insects.

No feeding observations were made of Little Rush Warblers but this species always dropped down into undergrowth when released after ringing, and the low position in the nets at which they were caught, both within the swamp and in the middle area amongst *Sesbania*, suggests that they were feeding very near to the ground. African Reed Warblers adopted various feeding strategies, occurring fairly low down within the papyrus, feeding amongst the stems, and also feeding at the edge in *Sesbania* trees, in the manner of Reed Warblers in willows *Salix* sp. in Europe.

Only one pair of Hunter's Cisticolas *Cisticola hunteri* was observed at the swamp edge, but the numerous Winding Cisticolas fed mainly in the undergrowth, at the base of trees and shrubs or walking out on to *Salvinia* in the drainage channel, feeding on insects in and on this floating carpet. These cisticolas generally occurred at the edge of the papyrus, feeding both on the bank, in the channel and within the area of flooded grassland. Sedge Warblers fed in a similar manner to *C. galactotes* on the *Salvinia* carpet, and at the base of papyrus and trees, but most observations of this species were in the two hours after dawn when they fed mainly in *Sesbania* trees near the swamp edge at heights up to 4–5 m. Great Reed Warblers were rarely observed feeding other than in the *Sesbania* trees.

Discussion

In this study, data indicated that there was considerable segregation of warblers at Naivasha. Winding Cisticolas occurred predominantly on the landward side of the swamp, feeding low down, and Lesser Swamp Warblers mainly at the lake edge. Great Reed Warblers occurred throughout the swamp and at various heights, but are, of course, much larger than the other species. The small Little Rush Warbler also occurred throughout but was most frequently caught on the landward side and only occurred at low levels. Other species, with the exception of Sedge Warblers, were caught in small numbers suggesting that swamp was not necessarily their preferred habitat. This is consistent with the different habitat preferences described by Pearson (1972) and Britton (1980), with Sedge Warblers being largely restricted to vegetation near water and other migrant *Acrocephalus* species occurring in a greater range of, often dry, habitats. Sedge Warblers

were common and apparently favoured a similar position in the swamp as Lesser Swamp Warblers, but the Palaearctic species, unlike the residents, also spent much time in trees at the swamp edge and on the bank.

In Nigeria, Aidley & Wilkinson (1987) caught three Palaearctic and three Afrotropical *Acrocephalus* species between September and May; the Palaearctic species comprised 85 per cent of total captures of warblers of this genus. In western Kenya, Britton (1978) found the impact of migrant *Acrocephalus* species on resident swamp birds to be minimal. He caught only one Sedge Warbler from September 1971 to November 1972. This contrasts markedly with the ratio of 1 : 2.5 (54 migrant *Acrocephalus* : 137 'resident' swamp warblers, i.e., *Acrocephalus*, *Bradypterus* and *Cisticola* spp.) at Naivasha in January and February 1990, and 1 : 2.7 (102 : 282) in early March.

Marked differences in body mass and bill-length between the commoner species of warblers (Table 1) might suggest that different prey items are taken, although smaller individuals of Lesser Swamp Warblers (Fig. 1) were similar in size to some Sedge Warblers. Likewise, smaller individuals of Winding Cisticola had a similar body mass and wing- and bill-length to Little Rush Warblers.

It is of interest that in western Kenya, Lesser Swamp Warblers appear to be excluded from the papyrus stands by Greater Swamp Warblers, but favour papyrus in the absence of their larger relative; but the same does not hold true for Winding Cisticolas in the absence of Carruthers' Cisticola. The former are birds of the swamp edge in both situations.

The observed differences in heights that different species of warblers were caught at appear largely to reflect the observed differences in feeding strategies. Sedge Warblers commonly fed high in *Sesbania* trees as well as down at water level, whilst cisticolas and Little Rush Warblers were skulking species, feeding and moving through vegetation near to the ground. Any pattern would be complicated by differences in behaviour when birds are courting and singing, or dispersing. Then they may be higher in the vegetation than when feeding. Certainly some species were singing in early March from the tops of the papyrus.

Britton (1978) found no evidence of vertical zonation in papyrus in eight species of warbler in western Kenya, and remarked that it was exceptional for any papyrus warbler to be caught above the second shelf of his mist nets. He therefore suggested that most warblers foraged near to the ground. However, he noted that some warblers were so similar in size that ecological separation was unlikely without habitat partitioning

Pambour (1990) found some evidence of vertical segregation between five passerines in a reed bed in southern France in the post-breeding migration period, but the three species—Reed, Sedge and Great Reed Warblers—all showed a similar vertical distribution. Their horizontal distribution was also similar, with most occurring near the lake shore, which Pambour suggested was due to the edge between the reed bed and lagoon forming a physical barrier and concentrating migrants, and possibly also to this outer edge, providing a greater diversity and abundance of prey. These reasons may also possibly explain why a high proportion of Lesser Swamp and Sedge Warblers were caught in the nets closest to the lake at Naivasha.

On the basis of the limited data from this and other studies, it would appear that the papyrus swamp warblers are largely segregated on size and habitat. The two species, Lesser Swamp and Sedge Warblers, that occur in the largest numbers in lakeside swamp, at least from January until March, and at similar heights, could compete, although the former is generally larger. The larger size of the African species might in itself be the

result of past competition with the closely related Palaearctic migrant.

Conversely, it may be that food is not a limiting factor and that during the late winter period (January to April) insects are sufficiently abundant so that several closely related species can coexist without competition or with minimal segregation. An increase in insects with the onset of the rains at the end of February would coincide with the peak passage of Sedge Warblers through Kenyan lakeside vegetation (Pearson *et al.* 1979). In the Serengeti, Sinclair (1978) found that Palaearctic migrants overlapped with related African species only where there was a local superabundance of food. As insects decreased in numbers, so the migrants dispersed into other habitats where they were not competing for available resources with closely related African species.

It would be helpful to have further information on the use made by birds of papyrus swamp and other types of emergent vegetation. Britton (1974) concluded that papyrus stands formed a homogeneous habitat supporting very few species of either residents or migrants, with the migrants feeding along the edge and hardly penetrating the interior of the swamp. By contrast, Pearson (1972) found that lakeside vegetation at Kampala (southern Uganda) supported higher densities of passerine migrants than cultivated bush away from the lake.

Data on seasonal fluctuations in invertebrates in the lakeside swamp at Naivasha would be very useful to show whether an abundance of food in late winter permits coexistence of warblers without competition. Further data on the use made of papyrus swamp by resident warblers throughout the year would also be of considerable interest and would help clarify whether the arrival of Palaearctic warblers in December and January affects their behaviour in any way. Additional data from April and May, when Sedge Warblers are most abundant in lakeside vegetation, would also be of value.

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